Wilson Bull., 91(4), 1979, pp. 551–574

VOCALIZATIONS AND BEHAVIOR OF THE WILLET

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While the vocal repertoires of several game species have been analyzed spectrographically (Collias and Joos 1953, Ellis and Stokes 1966, Stokes 1967, Williams 1969, Heinz and Gysel 1970, Samuel and Beightol 1973), other non-passerines have been largely neglected. The shorebirds (Charadrii) provide a possible exception. The flight-song has frequently been discussed in shorebird studies because of its importance in territorial behavior, and has been analyzed in detail by Heidemann and Oring (1976). Some recent studies have presented spectrographic analyses of the whole vocal repertoire of single species (Oring 1968, Forsythe 1970, Bursian 1971, Graul 1974, Jenni et al. 1974, Skeel 1978). This paper presents a spectrographic analysis of Willet (*Catoptrophorus semipalmatus*) vocalizations and describes their importance in the bird's biology. It includes comments on their etiology, functions and adaptiveness.

STUDY AREA AND METHODS

I studied Willets during 2 breeding seasons (June 1974 to August 1975), totalling over 400 h of observation. Additional observations were made in 1976, 1977 and 1978.

The principal study site, located ca. 3 km west of Amalga, Cache Co., Utah, consists of a seasonally wet alkali flat known as The Barrens. In the midst of The Barrens is a series of broad, shallow (≤0.5 m deep) ponds. Surrounding these artifically maintained Barrens' ponds are drier fields and pasturelands. Some additional observations were made on Willets in other parts of Cache Valley and at the Bear River Migratory Bird Refuge in Box Elder County, Utah.

Field observations were made with 7 × 35 binoculars and a 20× spotting scope, often from an automobile or portable blind. Vocalizations were recorded at a tape speed of 19 cm-sec^{-1} on a Sony TC-800B portable tape recorder with a F-26S cardioid microphone mounted on a 61-cm parabolic reflector. Spectrographic analysis was done at the FL-1 setting on a model 6061-B Kay Electric Company Sona-Graph. A Tandberg Model 15-41F tape recorder was used with the sonagraph. Frequency measurements were taken from spectrograms made at the narrow band-pass setting, and temporal measurements were taken from spectrograms made at the wide band-pass setting. All time-frequency displays used in the analysis were made at a normal playback speed of 19 cm-sec^{-1}, but some made at 9.5 and 4.8 cm-sec^{-1} were used to clarify temporal patterning of notes. The acoustical terminology of Davis (1964) is followed.

Since no adults could be color-marked, long-term recognition of individuals was impossible. However, some individuals could be followed for several hours on a given day. Accordingly, an effort was made to use recordings from scattered locations in the study area for the numerical analysis (Table 2) so the standard deviations would represent interindividual variability within the population. As with Tomkins (1965), I found no reliable way to distinguish the sexes other than by behavior.

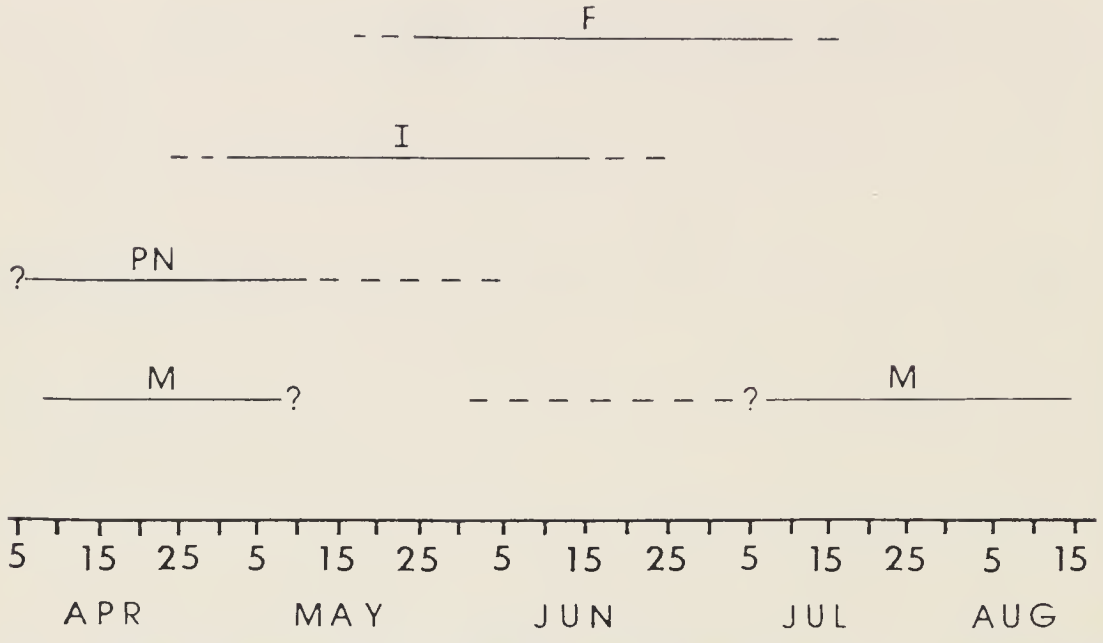

FIG. 1. Breeding schedule of the Willet in Cache County, Utah. (M = migration; PN = pre-nesting; I = incubation; F = fledgling care. Solid lines indicate periods based on observations; dashed lines indicate possible extensions based on calculations.)

RESULTS

Willets arrived in Cache Valley during the first week of April, with first arrivals seemingly paired. The breeding schedule of this population is presented in Fig. 1. Calls and their biological characteristics are summarized in Table 1, and a quantitative description is presented in Table 2. A discussion of each vocalization follows.

Pill-will-willet.—This loud and ringing call (Fig. 2A), from which the bird derives its common name, consists of 3 parts: *pill-*, which is a stuttered series of 3 to 5 ($\bar{x}$ = 3.30, SD = 0.46, N = 66) short notes, is separated from *-will-* by about 0.03 sec, and *-will-* is separated from *-willet* by about 0.04 sec. Once a bird consistently gave this call with the *wil-let* broken, and 2 birds gave it without the terminal syllable (hence, *pill-will-will*). The call has a harmonic structure with the fundamental (at about 1.1 kHz) and odd harmonics suppressed. The first overtone is emphasized.

This call has been likened in function to passerine song (Vogt 1938). If song is defined as "advertising the presence of a paired or unpaired male in breeding condition, as well as the existence of a defended territory" (Nottebohm 1975), it should be considered song. Vogt (1938) ascribed this call primarily to males, and I only heard it a few times from known females. On 1 May 1975, a female gave this call as a male approached her sexually (a successful copulation ensued). Evidence for an advertising function is given by the fact that Willets often gave this call in the absence of any obvious recipient or external stimulus. Von Frisch (1960, *in* Arm-

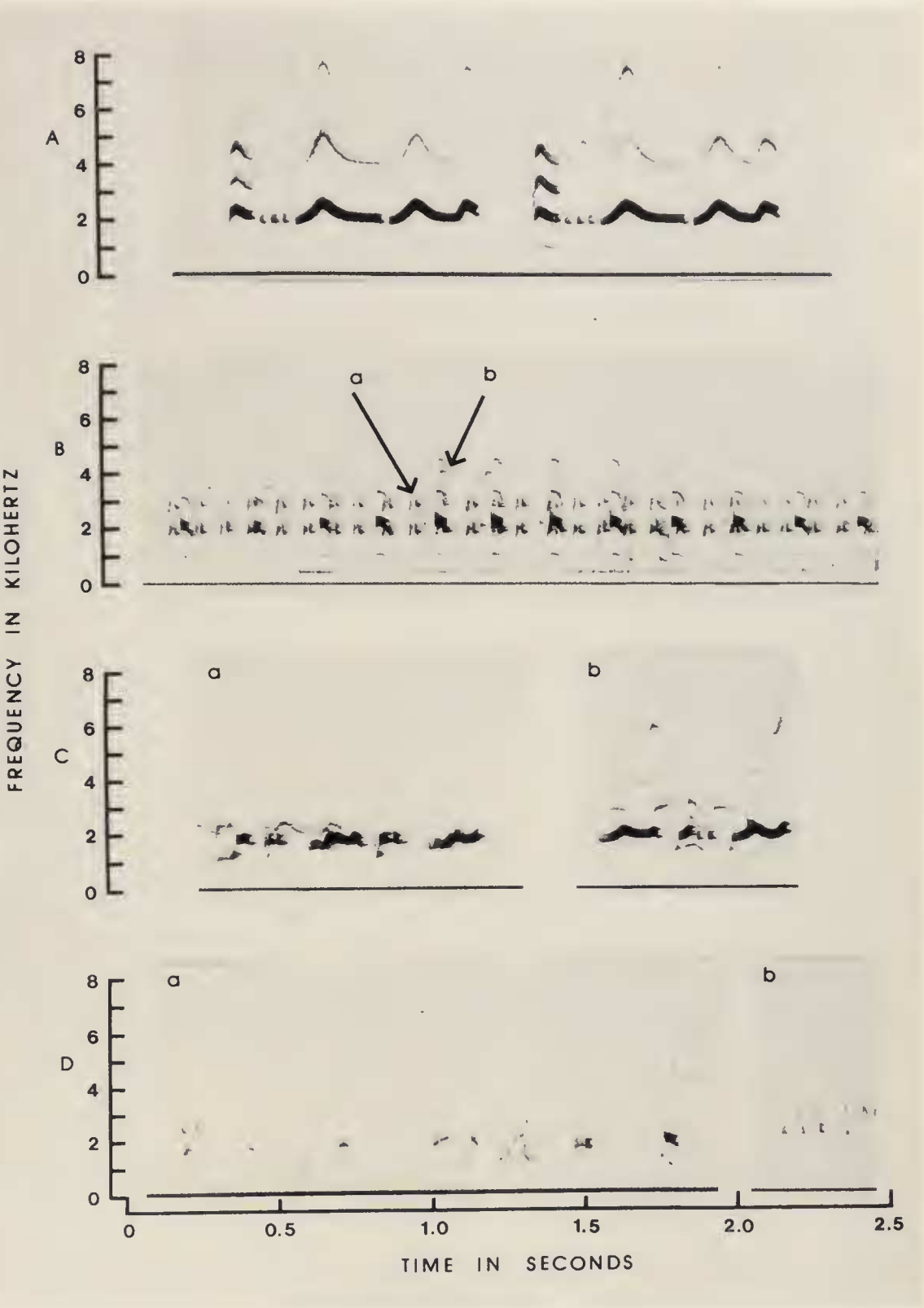

FIG. 2. Spectrograms of Willet vocalizations. A. Two *pill-will-willet* calls; B. a, *klik* calls and b, *dik* calls given simultaneously by 2 birds (see text); C. a, b, 2 examples of *hunker-hunk*; D. a, b, 2 examples of *cluck*.

TABLE 1

SYNOPSIS OF THE CALLS OF THE WILLET

Call	Sex of bird	Occurrence during annual cycle[a]	Etiology	Simultaneous behavior[c]	Function
Pill-will-willet	Both	PN through late F	Presence of conspccifics or disturbance on territory	*A* display; *T* wing-up display; erect stance	Proclamation of territory and mate; announcement
Klik	Male?	PN	Second Willet in proximity	*T* wing-flutter display	Epigamic
Dik	Female?	PN	Sexual approach of male Willet	Horizontal posture or walk/run away	Epigamic
Kyah-yah 1-, 2-, 3-, and 4-note variants	Both	Probably AY	Presence of conspecific	*T* activities (feeding, comfort); flight or taking flight	Contact, flight intention, flight enticement
Kleep high, medium, and low intensity	Both	Probably AY	Disturbance of individual, especially with respect to nest or young	Flight; *T* head-bobbing display; mobbing	General predator alarm
"Scream"	Both	Probably AY	Active presence of an enemy	Flight or taking flight; mobbing	Excitement
Cluck	Both	Probably AY	Conspecific in proximity	Flap-hop or wing-up display, or pause in *T* activity	Distance increaser
Hunker-hunk[b]	Both	Possibly AY	Some disturbance in the vicinity	Most often given on ground	?
"Warble"[b]	?	F?	Presence of potential predator in vicinity of young	Alert posture; young crouch?	Warning to young?
"Whistle"[b]	?	F?	?	Circling flight	?
Eeee	Both (Young)	F	Imminent danger to self	Active escape attempts	Distress

TABLE 1
CONTINUED

Call	Distance decreaser	Associated calls	Elicited by conspecifics	Answered by conspecifics	Calls given by conspecifics
Pill-will-willet	No	*Hunker-hunk*, *kleep*	Yes	Yes	*Pill-will-willet*, *hunker-hunk*, *kleep*
Klik	Yes	*Pill-will-willet*, *kleep*	Yes	?	*Dik*
Dik	?	*Pill-will-willet*, *kleep*	Yes	?	*Klik*
Kyah-yah 1-, 2-, 3-, and 4-note variants	Yes	*Kyah-yah* variants, *cluck*	Yes	Yes	*Kyah-yah* variants
Kleep high, medium, and low intensity	Yes	"Scream," *pill-will-willet*	Sometimes	Yes	*Kleep*, *pill-will-willet*, "scream"
"Scream"	No	*Kleep*, *pill-will-willet*	Sometimes	Sometimes	"Scream", *kleep*, *pill-will-willet*
Cluck	No	*Kyah-yah* variants	Yes	Yes	*Cluck*, *kyah-yah* variants
Hunker-hunk[b]	No	*Pill-will-willet*, *kleep*	Yes	Yes	*Pill-will-willet*, *kleep*
"Warble"[b]	?	*Pill-will-willet*	Probably not	No	?
"Whistle"[b]	?	?	Probably	?	?
Eeee	Yes	?	No	Yes	*Kleep*, "scream"

[a] PN = pre-nesting, F = fledgling, AY = all year.
[b] See text for further explanation.
[c] *A* = aerial, *T* = terrestrial.

Table 2

Numerical Description of Willet Vocalizations

Call	N	$\bar{x}$	±SD
Pill-will-willet			
Duration of call[a]	68	0.785	±0.039
Interval between calls	56	0.201	±0.088
Maximum frequency[b]	69	2.46	±0.09
Minimum frequency	69	1.79	±0.07
Klik			
Duration of call	64	0.037	±0.006
Interval between calls	57	0.056	±0.016
Average fundamental frequency[c]	45	1.03	±0.05
Average emphasized frequency	64	2.04	±0.05
Dik			
Duration of call	51	0.037	±0.012
Interval between calls	45	0.113	±0.044
Average fundamental frequency	43	1.16	±0.05
Average emphasized frequency	51	2.16	±0.06
Kyah-yah			
1-note variant			
Duration of note	15	0.301	±0.090
Interval between notes	3	0.677	±0.206
Average fundamental frequency	5	1.16	±0.05
Average emphasized frequency	14	2.24	±0.14
2-note variant			
Duration of first note	16	0.221	±0.083
Duration of second note	16	0.167	±0.049
Interval between first and second notes	16	0.051	±0.024
Duration of call	16	0.439	±0.137
Interval between calls	4	0.657	±0.326
Average fundamental frequency of first note	7	1.23	±0.10
Average emphasized frequency of first note	16	2.27	±0.12
3-note variant			
Duration of first note	18	0.139	±0.061
Duration of second note	18	0.125	±0.036
Duration of third note	18	0.119	±0.039
Interval between first and second notes	18	0.043	±0.028
Interval between second and third notes	18	0.044	±0.030
Duration of call	19	0.472	±0.140
Interval between calls	2	0.445	±0.035
Average emphasized frequency of first note	17	2.33	±0.14

TABLE 2
CONTINUED

Call	N	$\bar{x}$	±SD
4-note variant			
Duration of first note	5	0.136	±0.054
Duration of second note	5	0.140	±0.044
Duration of third note	5	0.118	±0.027
Duration of fourth note	5	0.114	±0.029
Interval between first and second notes	5	0.038	±0.024
Interval between second and third notes	5	0.046	±0.032
Interval between third and fourth notes	5	0.044	±0.026
Duration of call	5	0.630	±0.209
Interval between calls	2	0.695	±0.177
Average emphasized frequency of first note	6	2.30	±0.14
Kleep			
High intensity = interval < 2 × duration			
Duration of call	58	0.113	±0.041
Interval between calls	52	0.146	±0.052
Average fundamental frequency	55	1.29	±0.06
Average emphasized frequency	60	2.48	±0.13
Medium intensity = 2 × duration ≤Interval < 3 × duration			
Duration of call	63	0.094	±0.023
Interval between calls	58	0.229	±0.054
Average fundamental frequency	32	1.25	±0.07
Average emphasized frequency	67	2.37	±0.10
Low intensity = interval ≥ 3 × duration			
Duration of call	52	0.092	±0.017
Interval between calls	44	0.323	±0.073
Average fundamental frequency	38	1.31	±0.03
Average emphasized frequency	56	2.48	±0.10
"Scream"			
Attack			
Duration of call	38	0.191	±0.098
Interval between calls	33	0.183	±0.114
Average fundamental frequency	6	1.30	±0.00
Average emphasized frequency	38	2.50	±0.19
Flee			
Duration of call	26	0.348	±0.059
Interval between calls	21	0.200	±0.056
Average emphasized frequency	23	2.42	±0.08

TABLE 2
CONTINUED

Call	N	$\bar{x}$	±SD
Cluck			
Duration of notes	49	0.059	±0.015
Interval between notes	44	0.095	±0.089
Average fundamental (= emphasized) frequency	53	1.42	±0.18
Hunker-hunk			
Duration of individual notes	28	0.147	±0.067
Interval between individual notes	20	0.136	±0.157
Duration of note clusters	6	0.570	±0.183
Maximum frequency	8	2.06	±0.14
Minimum frequency	8	1.55	±0.19
"Whistle"			
Duration of first note	9	0.128	±0.004
Duration of second note	9	0.124	±0.005
Interval between notes	9	0.080	±0.016
Duration of call	9	0.334	±0.010
Interval between calls	9	2.84	±2.03
Maximum frequency	9	4.53	±0.14
Minimum frequency	9	3.39	±0.26
Eeee			
Duration of call	24	0.527	±0.080
Interval between calls	17	0.321	±0.128
Average frequency	24	4.56	±0.13

[a] All durations and intervals are in sec.
[b] All frequencies are in kHz.
[c] Average frequencies were determined by estimation of the frequency on either side of which lies half of the sound energy.

strong 1963) noted that the song-flights of a number of shorebirds may be elicited by different types of stimuli and might be termed "excitement flights." All authors have recognized the territorial function of *pill-will-willet*. When on territory, birds frequently gave this call (occasionally accompanied by a wing-up display) when another Willet flew by. Often the caller gave chase, especially if the intruder landed nearby.

I concur with Tomkins (1965) that this call is given frequently during the day or (occasionally) night during the pre-nesting period, less so during incubation, and only occasionally while escorting young. *Pill-will-willet* may be uttered from the ground or in flight. Howe (1974) noted that males and females (at least when a male is present) gave this call after landing in the territory and while holding both wings vertically for 2 or 3 sec.

Aerially, this call is given in song-flight (*sensu* Armstrong 1963: 136), a conspicuous performance which Vogt (1938) dubbed "spottying" because of its resemblance to the flight of the Spotted Sandpiper (*Actitis macularia*). This display is characterized by stiffly arched wingbeats which pass through a shallow arc (producing a hovering effect), alternating with periods of gliding on outstretched wings. It may occur at heights from about 10 m to those that make the Willet a mere speck to a human observer. The bird calls persistently, and there is no relationship between the undulating pattern of flight and the syllable delivered, as there is in the song-flight of the Red Knot (*Calidris canutus*) (Nettleship 1974). The performance is often terminated by a spectacular earthward swoop on outstretched wings. Sometimes the bird is silent during the final few meters of descent (Vogt 1938, pers. obs.) but, just as often, calling continues until the bird has landed and given a wing-up display. *Pill-will-willet* is sometimes given during direct flight, but even then it is usually alternated with the display flight. Its intermittent occurrence during mobbing sequences suggests that during times of stress it may be given as a displacement call. Alternatively, it may be released by the sight of other Willets that have joined the mob in the territory (I could never determine positively if it was the resident calling). As noted by Vogt (1938) this song-flight is highly contagious among neighboring Willets. When 1 bird began the display, up to 6 more Willets often were stimulated to do likewise. These cacophonous events were interjected between periods of silence. The birds flew in wide circles roughly delimiting their territories (on the order of 0.04 km^2), although they gravitated toward the nearest displaying neighbor. Sometimes a bird continued in a straight line until out of sight, crossing several territories as it went. Willet singing bouts sometimes lasted 5 min or more during the pre-nesting period, an individual engaging in 5 or more bouts per h.

Klik and dik.—These 2 calls (Fig. 2B) were transliterated to reflect their staccato nature and the fact that *klik* is a double-noted call and *dik* is a single-noted call. They are of approximately the same duration and frequency, but *klik* is repeated nearly twice as rapidly as *dik* (Table 2). Both have a harmonic structure, with the second harmonic emphasized.

Klik and *dik* were heard exclusively during copulation attempts (51 observations). Many of my recordings of these calls are of poor quality, but it seems that both calls were always given in such situations, even when mounting did not occur. The 2 calls were difficult to distinguish by ear, except when *dik* calls became very loud.

The literature is vague concerning the epigamic calls of Willets. The description by Nichols (1920) of a "kuk-kuk-kuk . . . in tern-like series from two mating birds" has been followed in later accounts (e.g., Bent

1929). Vogt (1938) described a rapid clicking which increased in tempo as the "male copulation note" and a "grunting eh-eh note" given by the female during copulation. Sonagrams reveal 2 structurally different notes which are out of phase. In 2 cases where it was possible to analyze recordings of copulation attempts from beginning to end, the sequence began with *klik* calls. Both ended with *dik* calls, grading into *kleep* calls. As neither resulted in mounting, I have inferred that *klik* was produced by the male (who appeared to initiate the episode) and that *dik* was produced by the female. However, even though females can be seen to open their bills at irregular intervals during copulation, the possibility that males produce both *klik* and *dik* with separate sound sources cannot be excluded without further evidence. The augmentation of the *klik* calls by *dik* calls explains the increase in tempo mentioned by Vogt (1938) as well as the pulsed sensation a listener receives (analogous to the beats produced by 2 simple tones of slightly different frequencies).

These calls may be repeated for up to 2 min or more as a male pursues an unreceptive female. Males employ a precopulatory wing display which has been called "wing-flickering" (Vogt 1938) or "wing-waving" (Tomkins 1965). Both the wing display and the copulatory notes are given until the act is completed. Near the end of the actual copulation, *dik* calls become louder and more irregular, often grading into *kleep* calls.

An interesting feature of Willet copulation notes is their conspicuousness. Vogt's (1938) statement that they could be heard at distances exceeding ⅛ mile (0.20 km) is accurate. I estimated that at times they could be heard at twice that distance. It is unusual for a bird to make itself so conspicuous at such a vulnerable time—one when most species utter calls that are difficult to locate (Armstrong 1963:13). Sympatric shorebirds, including the Long-billed Curlew (*Numenius americanus*), Wilson's Phalarope (*Phalaropus tricolor*), Killdeer (*Charadrius vociferus*), American Avocet (*Recurvirostra americana*), and Black-necked Stilt (*Himantopus mexicanus*) give no audible calls during copulations (pers. obs.). Descriptions of the copulation calls of other tringines (Haverschmidt 1963, for the Black-tailed Godwit [*Limosa limosa*]; Nethersole-Thompson 1951, for the Greenshank [*Tringa nebularia*]; Oring 1968, 1973, for Solitary Sandpiper [*T. solitaria*] and Green Sandpiper [*T. ochropus*]) do not emphasize loudness or locatability. Both *klik* and *dik* possess the characteristics of short time span and wide frequency range which make them easy to locate (Marler 1955), and the male's wing display further increases the pair's conspicuousness. Although Willets are strong and swift fliers, wintering flocks do suffer from predation by raptors (Page and Whitacre 1975). Thus the conspicuous copulation seems at least potentially maladaptive. If so,

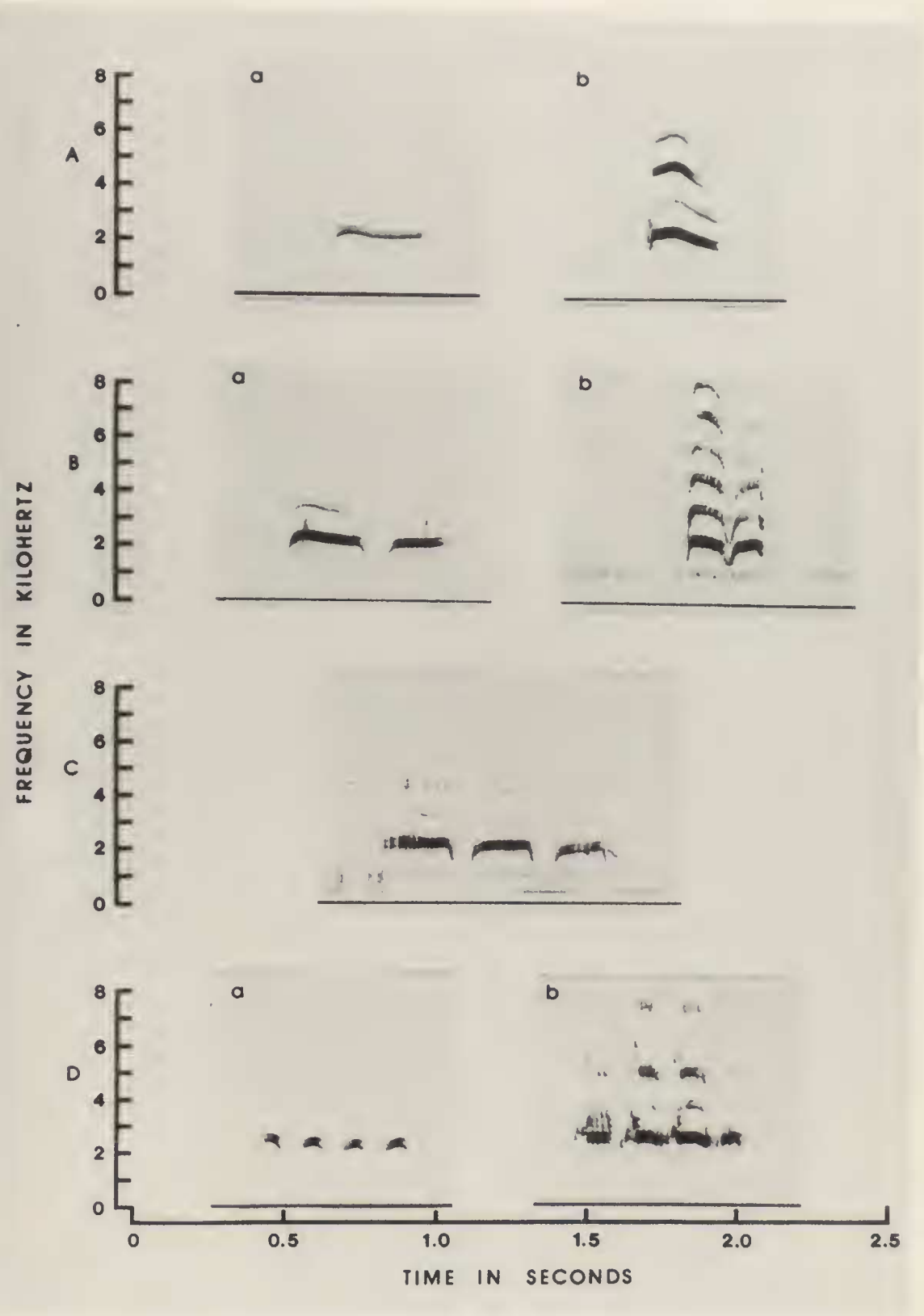

FIG. 3. Spectrograms of Willet *kyah-yah* calls. A. a, b, 2 examples of 1-note variant; B. a, b, 2 examples of 2-note variant; C. 3-note variant; D. a, b, 2 examples of 4-note variant.

counter-selection must be balanced by other selection pressures. What these pressures might be is open to conjecture.

Courtship calls often manifest a mingling of attack, escape, and sexual tendencies (Armstrong 1963:14), i.e., they may represent ritualized agonistic behavior. Both *klik* and *dik* are structurally similar to *kleep* calls, which denote alarm and intolerance. They often grade into *kleep* calls and at times are difficult to distinguish spectrographically. This difficulty is illustrated by the fact that Vogt (1938) described the call given by a male at a border confrontation as what I interpret to be *kleep*, whereas Howe (1974) implicated *klik* in the same situation. Since all other wing displays in Willets seem to contain an aggressive component, I suggest that the entire male copulatory display represents ritualized aggression. Females, when receptive, assume the antithetical appeasement posture with body horizontal and head lowered. When 1 Willet, uttering *klik* calls and wing-waving, approaches another Willet (I usually did not know the sexes of the birds with certainty), the result is either copulation, a chase, or a fight.

Kyah-yah.—This call (Fig. 3) exhibits a great deal of structural variability. It occurs as single- and multiple-note variants, and so I have designated 1-, 2-, 3-, and 4-note variants. It was recorded twice as a 5-note call. Individual notes ranged from 0.07 sec to 0.44 sec in duration, with multiple-noted calls tending to have shorter notes. Second, third, and fourth notes tend to be progressively shorter in duration. They also frequently drop about 0.1 kHz in frequency. Notes are generally of constant frequency but often tail on and off, and sometimes a small inflection is present. A harmonic structure is present with intervals of about 1.1 kHz.

One feature of this call that makes interpretation difficult is the frequent appearance of rapid modulations or frequency displacements of portions of the notes. Virtually any part of any note may be displaced, always upward (higher frequency), up to about 1.0 kHz. Some fragmentation can be seen in the first note in Fig. 3Db. Such modulation might be produced by changing tension in the tympanic membrane, changing pressure in the clavicular air sac, insertion or withdrawal of the external labium in the syringeal passage, or by a combination of these effects (Greenewalt 1968:101). This phenomenon is even more pronounced in the Willet "scream" call, in which it denotes excitement. One is reminded of the cracking of a human voice under stress or excitement.

The variability of *kyah-yah* is expressed in some very different sounding calls. I believe the following (quite aptly named) calls attributed to Willets in the literature are referable to *kyah-yah*: *kiyuk*, *ki-yi-yuk*, *kree-uk* (Nichols 1920); *k-a-aty*, *teee-eeer* (Vogt 1938); *kay-ee* (Peterson 1961); *phwee-hoo* (Tomkins 1965); *whee-wee-wee*, *whee-hoo* (Palmer 1967).

Possibly with a large sample size some functional subdivision could be

made on the basis of structure for this call. *Kyah-yah* is exchanged by 2 or more birds which meet in direct flight. It is given when 1 or more birds fly over other Willets (usually first given by the flying individual and often returned by the bird on the ground, especially when it takes flight to follow). Two or more Willets, or groups of Willets, exchange plaintive *kyah-yah* calls when separated by some distance while feeding or loafing. Birds within large flocks of Willets exchange these calls as if restless, their rate of delivery increasing until the whole flock takes flight amid a volley of multiple-noted variants. During interludes in mobbing, 2 Willets (perhaps members of a pair) often perch on fenceposts and exchange strident 1-note variants.

Thus *kyah-yah* serves as a greeting and contact call, an indication of flight intention, and a flight enticement call which seems important in eliciting a following reaction. A sample of recordings of these calls suggests that an increasing number of notes reflects an increasing motivation to fly. Birds engaged in terrestrial activity gave 1-, 2-, 3-, and 4-note calls in 22, 11, 5, and 0 instances, respectively. Birds engaged in aerial activity gave them in 0, 10, 19, and 6 instances. The difference is highly significant ($\chi^2 = 36.15$, 3 df, $P < 0.001$). A rigid distinction cannot be made between alarm calls and calls indicating that a bird is taking flight for one reason or another (Armstrong 1963:16). Indeed the 1-note variant of *kyah-yah* often seems to communicate a sense of uneasiness among the birds. And the calls given in the mobbing context described above are likely to have an alarm component. One-note *kyah-yah* calls of Willets are structurally similar to 1-note *wheet* calls of the Long-billed Curlew, which signify anxiety and alarm (Forsythe 1970).

Kleep.—This is a double-noted call (Fig. 4), rising slightly on the first note and falling on the second. Its harmonic components span a broad frequency range, with the fundamental sometimes being suppressed. The amplitude and length of notes are variable, which accounts for the variety of descriptions in the literature: *wek*, *kerwek*, *piuk* (Bent 1929); *dik* (Vogt 1938); *kip* (Peterson 1961); *kleep*, *klip* (Tomkins 1965).

Kleep is one of the most frequently heard calls during the breeding season, especially during the incubation and fledgling care periods. The fact that it was already being given when Willets arrived in the spring has led me to speculate that it may occur year-round (Table 1). However, it is probably rare outside of and may be restricted to the breeding season as is the similar *ki-keck* call of the Long-billed Curlew (Forsythe 1970).

Bent (1929) called this the "usual note" of the Willet, which testifies to the conspicuous behavior of the bird as it *kleeps*. It is given by birds which are obviously disturbed (other activities are ceased and an alert posture is assumed), and is used in mobbing. The call is vehement, piercing, and

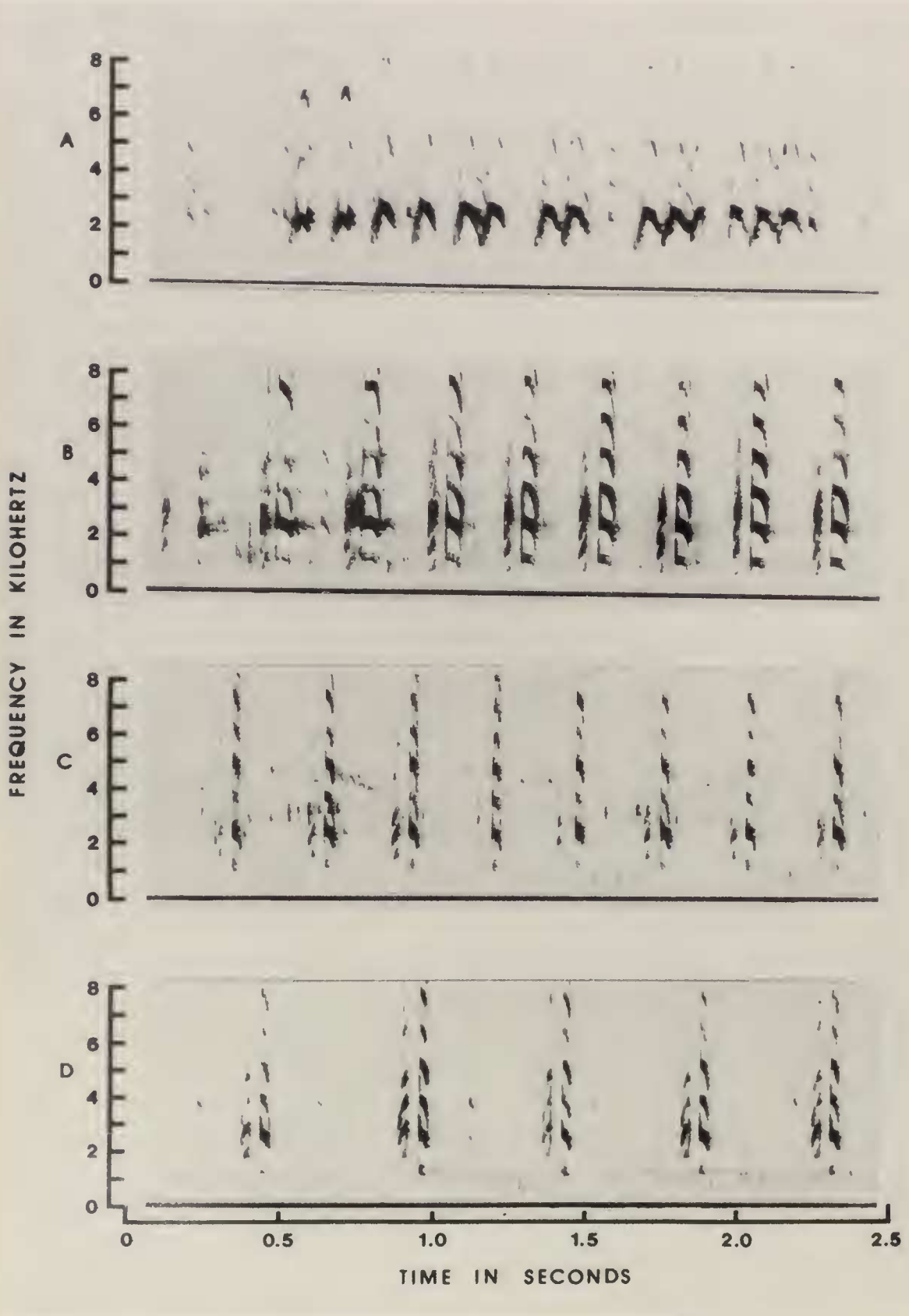

FIG. 4. Spectrograms of Long-billed Curlew and Willet vocalizations. A. Long-billed Curlew *ki-keck* call (1-, 2-, and 3-note variants); B. Willet high intensity *kleep* call; C. Willet medium intensity *kleep* call; D. Willet low intensity *kleep* call.

incessant. With brief pauses it may be repeated by mobbing birds for over an hour. Mobbing, as practiced by Willets, is a very noisy event. In its most intense form it consists of what Hamilton (1975) has called "dive-bombing displays" for American Avocets and Black-necked Stilts. As noted by Tomkins (1965:161), however, there is little actual physical contact involved when Willets mob. This may be related to the fact that shorebirds have sensitive bills (Willets and 8 other species I have handled usually avoided bill contact and almost never bit or pecked at me), but their bluffing is impressive. Only once, when a few feathers drifted down from the back of a Marsh Hawk (*Circus cyaneus*), was I certain that a Willet had made contact.

Willets have been said to "call from a calling post" (Forsythe 1970) and to "bob their heads when walking or standing" (Palmer 1967). Both activities are associated almost exclusively with *kleep* calls and a state of alarm. It is not uncommon for temperate-latitude scolopacids to perch on poles, wires, or in trees (pers. obs.). Head-bobbing consists of a violent backward jerking of the head while keeping the bill parallel to the ground. This is an anxiety movement typical of many species of Charadrii (Maclean 1967, pers. obs.). Apparently the behavior of the Willets, as well as the structure of their calls, is designed to attract attention.

Many species of birds reveal degrees of alarm or the imminence of danger by varying the loudness or rapidity of their calls (Armstrong 1963:17). This is true on both counts for Willet *kleep* calls. Following this idea I arbitrarily divided *kleep* into 3 categories based on calling rate (Table 2). A sample of recordings suggests that these categories do represent high (interval between calls $< 2 \times$ duration of calls), medium (interval between calls 2–3 $\times$ duration of calls),and low (interval between calls $> 3 \times$ duration of calls) intensity alarm responses. Birds engaged in terrestrial activity gave the high, medium, and low responses in 3, 11, and 10 instances, respectively. Birds engaged in aerial activity gave them in 11, 6, and 1 instances. The difference is significant ($\chi^2 = 12.81$, 2 df, $0.001 < P < 0.005$). Aerial activity is equivalent to active mobbing and dive-bombing, and is thus a higher-level response. Two of the 3 birds giving high intensity *kleep* calls terrestrially were also head-bobbing vigorously from fenceposts and took flight shortly after. In other studies, too, calling rate has been associated with flight motivation (Andrew 1961) and mobbing intensity (Cully and Ligon 1976).

The following potential predators of Willets, their eggs, or young have been observed to elicit mobbing from Willets on my study area: humans, dogs, striped skunks (*Mephitis mephitis*), California Gulls (*Larus californicus*), Ring-billed Gulls (*L. delawarensis*), Marsh Hawks, Swainson's Hawks (*Buteo swainsoni*), Short-eared Owls (*Asio flammeus*), Black-billed

Magpies (*Pica pica*), Common Crows (*Corvus brachyrhynchos*), and Common Ravens (*C. corax*). Other predators I saw in the area were Great Horned Owl (*Bubo virginianus*), long-tailed weasel (*Mustela frenata*), red fox (*Vulpes fulva*), and common garter snake (*Thamnophis sirtalis*).

Mobbing is an important activity during the fledgling care period. In 1975 I first noted mobbing behavior on 12 May and saw it last on 10 July. The parents stand like sentinels, with the chicks usually somewhere between them. One pair, escorting chicks on the afternoon of 23 June 1975, averaged 4 chases per h of gulls and hawks (observation time = 3 h). A few observations of Common Crows and Black-billed Magpies taking great interest in the locations from which mobbing Willets flew up suggest that some predators may learn to key on mobbing behavior.

Both Vogt (1938) and Tomkins (1965) noted that Willets mob in groups. This is facilitated by the breakdown of territorial boundaries after hatching (Tomkins 1965:160). I saw little hostility between Willets at this time. Ten or more adults may participate in mobbing, with recruits sometimes coming from a considerable distance.

Though it seemed that only breeding birds mobbed actively, apparent nonbreeders and even fledged juveniles were sometimes attracted to mobbing scenes. They would fly in wide circles or land and walk about in the grass. Though Willets are said not to have a distraction display after hatching (Tomkins 1941), I often became confused as to which gray bird running through the grass was the fledgling, and I suggest that the very presence of all those birds constitutes an effective diversionary display (*sensu* Armstrong 1949).

Long-billed Curlews often join these mobbing groups. In my notes I recorded 8 observations of Willets joining other Willets and 5 observations of curlews joining Willets. In addition I recorded 3 instances of Willets joining curlews and 2 instances of curlews joining other curlews. Rarely, other species such as American Avocets, Black-necked Stilts, and Red-winged Blackbirds (*Agelaius phoeniceus*) participate. Both the breeding ranges (A.O.U. 1957) and habitats (pers. obs.) of Willets and Long-billed Curlews overlap broadly. Thus adults and especially their eggs and young are endangered by the same predators. It would be adaptive for individuals of either species to respond to the mobbing activities of other birds as well as to the predators themselves (secondary and primary responses, respectively, of Altmann 1956). This would (1) keep them apprised of the whereabouts of predators in the area, and (2) drive those predators out of the area. Group mobbing by Willets and Long-billed Curlews has been noted independently by D. M. Forsythe (pers. comm.) and myself in northern Utah, and by R. S. Sharpe and T. K. Bicak (pers. comm.) in western Nebraska.

The curlew *ki-keck* call shares a structural similarity with the Willet *kleep* call (Fig. 4A,B). Both calls are loud, have a sudden onset, and cover a broad frequency spectrum, and are thus easy to locate (Marler 1955). Resemblances of this kind have been interpreted as an example of evolutionary convergence in the mobbing calls of passerines (Marler 1959). It is unclear whether *kleep* and *ki-keck* have converged or reflect phylogenetic affinities. Furthermore, it is uncertain whether the observed interspecific responses result from auditory cues or visual ones, as the form of mobbing displays in the species is also similar. However, I believe the most reasonable hypothesis is that vocalizations attract attention to a general area and visual cues reveal the bird's precise location. Whether the responses are learned or built-in might be elucidated by further observations and playback experiments on allopatric populations.

"*Scream.*"—This call (Fig. 5Ab,B,C) is quite variable, especially in note duration. It comprises a single note which begins and ends gradually, and consists of a relatively narrow frequency band. Sometimes harmonic elements appear. But most striking is the rapid and irregular (and unpredictable) frequency modulation which breaks it into a multiple-note call. This phenomenon was discussed earlier for the *kyah-yah* call. The form of the call is remarkably similar to a basso *eeee* or chick distress call (compare Fig. 5, C and D). This similarity, along with the contexts in which it is given, suggests that "scream" may be derived from *eeee*. This is compatible with evidence that in a number of species (including the Eurasian Curlew [*Numenius arquatus*]) the vocabulary of calls has expanded from the calls of the chicks (Armstrong 1963:18). Forsythe (1970) thought that the *pert* call of Long-billed Curlew embryo-chicks developed into the adult *ki-keck* call. It is apparent in some "scream" calls that the Willets were employing 2 separate sound sources (overlapping notes of unrelated frequencies are present).

The situations in which "scream" is given indicate that it reflects a high degree of excitement. Twice Willets uttered these calls as I seized them. Many birds give similar calls in this context (Armstrong 1963:17), and they are likely to be effective in startling a predator into loosening its grip. I have arbitrarily divided this call into 2 categories, based on the apparent motivation of the calling bird. "Scream" attack occurred in such situations as when a pair of Willets mobbed a Short-eared Owl on 12 May 1975 (Fig. 5Ab); when 5 Willets, 2 Long-billed Curlews, and a Red-winged Blackbird mobbed a Marsh Hawk on 22 June 1975; and when 1 Willet mobbed a flock of Common Crows on 10 July 1975. "Scream" flee was recorded when a Willet was attacked by a territorial male Red-winged Blackbird on 14 April 1975 (Fig. 5B); when a long-tailed weasel nearly captured a Willet on 12 May 1975; and several times when 1 apparently

startled Willets into flight. These 2 types of "scream" calls (Table 2) are separable on the basis of call duration ($t = 7.33$, $P < 0.001$) but not by interval between calls ($t = 0.63$, NS) or average frequency ($t = 1.92$, NS).

One reason for the shorter duration of "scream" attack calls is that they often grade into *kleep* calls during mobbing. "Scream" attack and *kleep* calls have the same average emphasized frequency ($t = 0.61$, NS) and similar intervals between calls ($t = 2.04$, $0.01 < P < 0.05$), but differ in call duration ($t = 5.39$, $P < 0.001$). Tomkins (1965) mentioned that *kleep* sometimes approaches a scream. There are probably elements of aggression and distress in both "scream" attack and "scream" flee. "Scream" seems, more than anything else, to be a quality of voice which is related to extreme excitement.

Cluck.—This call (Fig. 2Da,b) is a staccato series of notes which is quite variable in all temporal components. It is given in social contexts which indicate that its major function is that of a distance increaser. For example, birds *cluck* as they feed or move about among other Willets. Observations on flocks showed that it is given by individuals that appear annoyed by conspecifics, and that it causes those conspecifics to move away slightly. Frequently it is accompanied by a flap-and-hop display or a wing-up display, both of which serve to clear more space for an individual in a dense flock. American Avocets and Black-necked Stilts also employ a flap-and-hop display when feeding in tight flocks if neighbors approach too closely (Hamilton 1975:32).

Cluck is a subdued sound, inaudible beyond about 25 m. Consequently it is difficult to obtain good recordings without putting the entire flock to flight. But when minor altercations occur within flocks, the calls become louder as they grade into *kleep* calls. This supports the contention that *cluck* has both aggressive and alarm components. One gets the impression that a Willet is muttering *kleep* calls. For *cluck* also the calling rate seems to be directly related to the proximity of conspecifics and the degree to which the bird is agitated.

Hunker-hunk.—This call (Fig. 2Ca,b) is unusual in that it may not have communication value, although the possibility that *kleep* and *pill-will-willet* calls given by conspecifics were responses to it cannot be excluded. It is clearly composed of a series of fragments of the *pill-will-willet* call. These fragments are highly variable in structure and may occur in a different sequence than they would in *pill-will-willet* (Fig. 2Cb). The series of fragments or note clusters contain from 2 to 5 notes ($\bar{x} = 3.00$, SD = 1.10, N = 6). Birds may give the *hunker-hunk* call intermittently for 15 min or more.

Hunker-hunk is a moderately loud call, but does not seem to be directed toward other birds. Rather, it seems to be an expression of conflicting

tendencies within the bird. It is heard most often during the pre-nesting and incubation periods, when Willets are strongly motivated to give aerial displays. It is probably rare, if it occurs at all, in the nonbreeding season.

A feeding Willet frequently gives this call when a neighbor begins an aerial display, thereby revealing an inclination to join the performance. The opposing urge usually seems to be feeding. Depending on which is more compelling at the moment, a Willet either walks along feeding, occasionally raising its head to utter *hunker-hunk* calls, or launches into the air calling *pill-will-willet*. Willets landing to feed after lengthy aerial displays sometimes give this call, and after a period of feeding, they often give a few *hunker-hunk* calls before beginning the next aerial display.

"*Warble.*"—This call was heard only 3 times, and I was unable to record it. On 21 June 1975 at 18:30 I watched 2 adult Willets and 1 downy chick feeding in a wet pasture. For about 30 min the adults fed toward me, always about 40 m apart and with the chick always between them. When they were about 20 or 30 m from me, I heard 1 adult give a rapid "warble." The call was repeated twice in the next few minutes. After the first call, I noticed that the chick had crouched. The next time I heard the call I saw that the chick was up and feeding again. The call was given again, and the chick crouched again, as I walked into the field (thus making it impossible to ascertain whether it was the call or the observer that caused the chick to crouch).

On each of the 3 observations of "warble," it graded into 1 or 2 terrestrial *pill-will-willet* calls. Spectrographic analysis might show that it is referable to *hunker-hunk* (which it resembled, to my ear), but I have considered it a distinct call because of its apparent function in warning the young.

"*Whistle.*"—This call, shown in Fig. 5Aa among *kleep* calls of an adult which was mobbing me, is a high-pitched 2-noted whistle. It was recorded only twice. On 2 July 1974, at 19:00 as I restrained a downy chick, 1 adult was persistent in mobbing me. One other Willet, which I identified as a juvenile, circled overhead as though mobbing, but remained silent except for a few "whistle" calls. This continued for about 30 min, and I recorded about 15 "whistle" calls. On 2 July 1977, 2 fledged juveniles (with no attending adults) exchanged a few of these calls as I observed them from approximately their normal flight distance. Thus "whistle" may function as a contact or alarm call for juveniles.

Eeee.—This call (Fig. 5D) is given only by young in the preflight stage. Its structure is such that it attenuates rapidly and is difficult to locate (Marler 1955). I heard it only from chicks that were in imminent danger (from me). A chick trapped in the open ran until it was about to be caught, then resorted to *eeee* calls. When held in the hand, chicks always gave

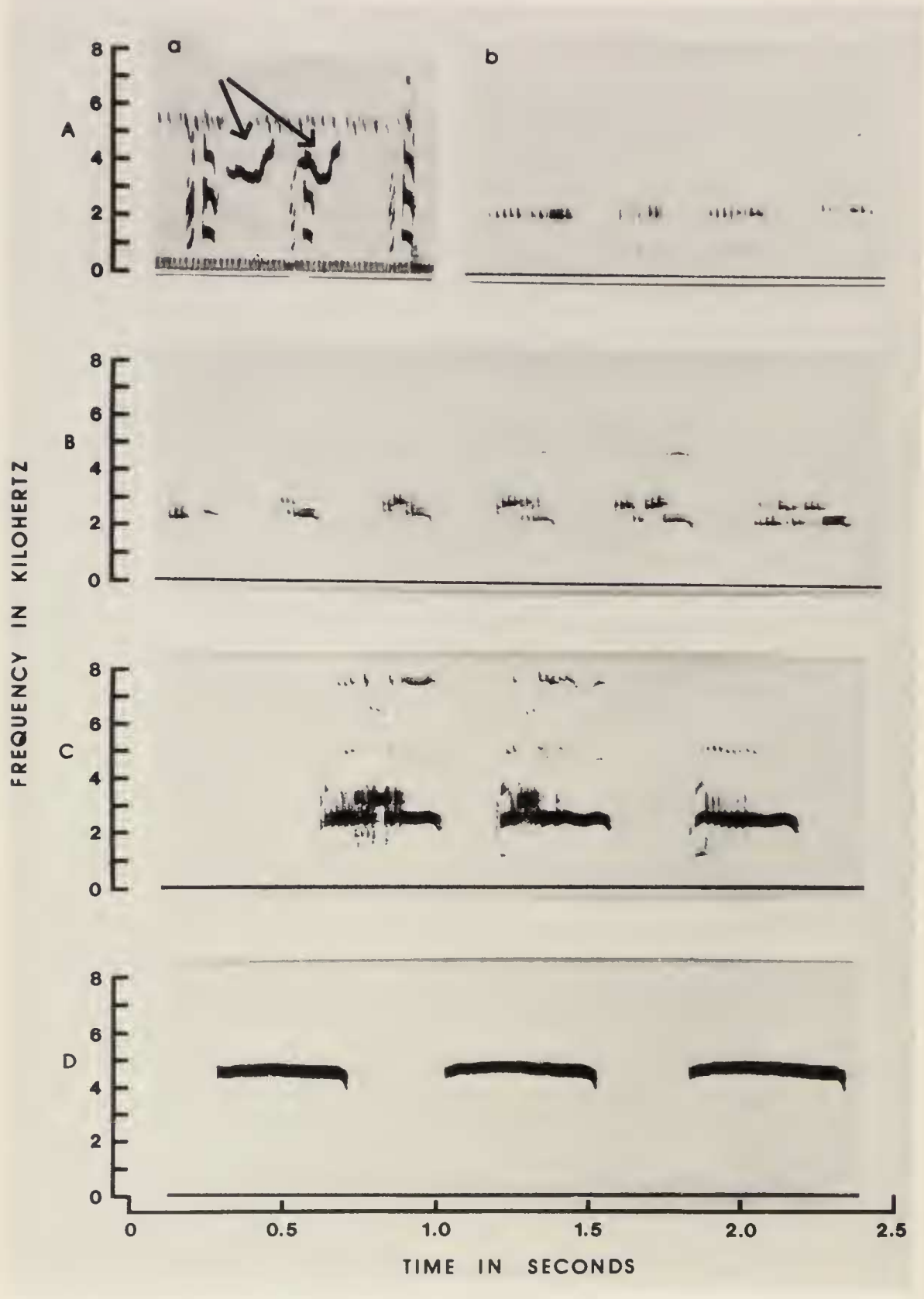

FIG. 5. Spectrograms of Willet vocalizations. A. a, "whistle" call and b, "scream" attack; B, C. 2 examples of "scream" flee; D. *eeee* call.

this call. On 21 June 1975, I watched a chick feeding and mentally marked the spot where it crouched as I approached. Its camouflage was so good that it took me over 10 min to locate it on the open field. Not until I held it high off the ground did it begin to squirm and utter *eeee* calls. When I released chicks, they usually became silent as they ran into the grass. Thus chicks devote their energies to escape until they are actually or very nearly caught. Their major means of escaping predators is hiding at the first alarm of the watchful adults, and then relying on the adults' mobbing and diversionary tactics.

The effect of *eeee* calls on adults is to heighten their level of excitement. *Kleep* calls become more intense, "scream" calls more frequent, and dive-bombing more vigorous.

Tomkins (1965) thought that the "thin wiry call" of young chicks served to keep the brood together and to keep the adults apprised of their location. The poor locatability of *eeee* calls makes me skeptical about such a function. In my experience *eeee* serves as a distress call which seems to elicit harassment of intruders from other Willets.

DISCUSSION

I have recognized 10 adult vocalizations and 1 chick vocalization for the Willet. Previous verbal descriptions have included 10 adult (Vogt 1938) and 1 chick (Tomkins 1965) vocalizations. However, I am unable to account for 4 of the 10 calls described by Vogt: "*yoicker-yoick*," "compulsion note," "a note that suggested the sound made by ruffling a deck of cards," and "contact note."

At least 4 of the Willet vocalizations identified in this study serve to decrease distance between conspecifics, and at least 4 do not (Table 1). Except for *cluck*, which operates only at close quarters, those not decreasing distance (*pill-will-willet*, "scream," and *hunker-hunk*) are probably rare outside the breeding season in this gregarious species.

Willets have vocalizations corresponding to about 7 of the 12 broad categories for signal function identified by Smith (1969). These are: identification, probability, general set, locomotion, attack, escape, and copulation. If flight enticement (*kyah-yah*) can sometimes be considered play initiation, the social play category would also be represented. The frustration category may be expressed by a number of vocalizations, but along with the nonagonistic subset, association, and bond-limited subset categories, it is probably conveyed largely by visual means.

Willets have vocalizations which correspond to at least 6 of the 10 functional categories listed by Thorpe (1961:17). That is, they have calls that I consider to be distress calls, territorial-defense calls, flight calls, flock calls, aggressive calls, and general alarm calls. I did not distinguish any

specialized alarm calls, pleasure calls, food-finding calls (Thorpe 1961:24), or nest calls. But Vogt (1938) described a call that may be a nest call.

Where communication purposes are adequately served, acoustic signaling should be favored over visual signaling because it is energetically more efficient (Wilson 1975:236). But open habitats are a difficult environment for sound propagation, due largely to wind-speed and temperature stratification. These conditions diffract the sound wave-front upward, producing a soundless area or "shadow zone" effect which can be erased if a bird calls from as little as 3 to 7 m above the ground (Morton 1975). Willets perform their song-flights at a minimum of 10 m, thus increasing their broadcasting effectiveness. This, along with the need for a better view, may also help account for the tendency of Willets to use elevated perches for sounding alarm (*kleep*) calls. Song-flight is a nearly universal characteristic of tundra and open country birds (Armstrong 1963:221).

Morton (1975) predicted that open country birds should not base information transfer on sound frequency (which is easily distorted by the above-mentioned environmental conditions). Instead he suggested that information coding should be based on temporal components, which remain little affected as long as the sound is audible. The length and spacing of notes of the Willet are more variable than their frequency. Most Willet vocalizations have emphasized frequencies of about 1.5 to 2.5 kHz, and therefore a relatively low attenuation rate. Only "whistle" and, to a lesser extent, *pill-will-willet* exhibit any appreciable frequency changes. The signal content of both *kyah-yah* and *kleep* has been shown to vary on the basis of temporal differences. And *klik*, *dik*, *cluck*, and *kleep* seem to be related structurally, but have marked temporal differences.

A refinement of Morton's interpretations (Marten and Marler 1977; Marten et al. 1977) generated similar predictions relevant to the maximization of sound transmission by Willets. The birds should: (1) vocalize from more than 1 m above the ground; (2) use low frequency sounds of approximately 2 kHz; and (3) produce loud sounds with the energy concentrated in a relatively narrow frequency band. These predictions are upheld. Thus both the behavior of Willets and the structure of their vocalizations show evidence of having evolved under the selection pressures of an open country habitat.

SUMMARY

Free-living Willets were studied during the breeding seasons of 1974 and 1975 in Cache County, Utah. A spectrographic analysis is presented for the 1 chick and 10 adult vocalizations recognized in this study, and a numerical and a biological description is given for each call. The song-flight, copulatory behavior, and antipredator behavior are discussed.

The vocal repertoire of the Willet is discussed in terms of its adaptiveness in an open

country habitat. It is suggested that the information of Willet sound signals is encoded primarily in temporal rather than frequency components.

ACKNOWLEDGMENTS

I wish to thank Keith L. Dixon for advice and criticism of all facets of this study, and for suggesting it in the first place. Dennis J. Martin contributed many ideas and much technical assistance, and Dennis M. Forsythe exchanged observations on shorebirds. The manuscript has benefited from critical readings by Lewis W. Oring, Marshall A. Howe, Allen W. Stokes, and Ivan G. Palmblad. Jack B. Parson granted access privileges to the Barrens ponds, and Hans A. Hansen granted access to the surrounding fields. It is a pleasure to express my gratitude to all of these individuals.

This study was supported by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and in part by a Utah State University Research Fellowship.

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DEPT. OF BIOLOGY UMC 53 AND THE ECOLOGY CENTER, UTAH STATE UNIV., LOGAN, UTAH 84322. ACCEPTED 29 SEPT. 1978.